

SOME OBSERVATIONS ON *SARCOPHILUS IANIARIUS* AND THE EVOLUTION OF *SARCOPHILUS*

by

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Three populations of *Sarcophilus*, a modern one from Tasmania, a sub-fossil one from Mt. Hamilton, Victoria, and a fossil one from Strathdownie, Victoria, as well as some additional sub-fossil and fossil specimens are analysed using quantitative and qualitative methods. Analyses of dental measurements show that there are some differences in both size and proportions between large and small forms of *Sarcophilus*. However, these are no greater in extent between fossil *S. ianiarius* and the modern form than between the latter and sub-fossil conspecifics from Mt. Hamilton. Analysis of the few postcranial remains suggests that large fossil *S. ianiarius* had a relatively more robust skeleton than the smaller modern form. Dental wear in the sample from Strathdownie is analysed and discrete wear stages are identified. This suggests that deposition at this site was either a singular event or was seasonal. Taxonomically, the quantitative data indicate that all forms studied are conspecific. The valid name for this single species of *Sarcophilus* is *S. ianiarius* Owen, 1838. The nominate subspecies is the large fossil form, *S. i. harrisii* is the modern form from Tasmania, and a new subspecies, *S. i. dixonae* is erected for fossil and sub-fossil specimens identical in size to the modern form. A further subspecies, smaller than the modern form, is identified but not named. It is noted that, due to population events in the recent past, modern *Sarcophilus* from Tasmania is of equivocal status relative to the evolution of the genus. A hypothesis of the interrelationships of the forms studied is presented in a cladogram.

INTRODUCTION

Fossil material referred to the genus *Sarcophilus* has been known for nearly 150 years. Finds have been described from localities of late Pleistocene and Holocene age all around Australia. They include specimens equal in size to the living Tasmanian devil, *S. harrisii*, specimens significantly larger than the living form, and specimens significantly smaller than this. The larger specimens have generally been referred to a separate species, *S. ianiarius*, which was first described from Wellington Caves, New South Wales, by Owen (1838; cf Mahoney and Ride 1975). The history of study of fossil *Sarcophilus* has been discussed by several authors, including Marshall (1973a) and Dawson (1982), and the reader is referred to these publications for further information. Dawson's (1982) paper also represents the latest review of fossil morphotypes of *Sarcophilus* and their taxonomic status.

The purpose of this paper is to examine what is currently known concerning the late Pleistocene to Holocene history of the genus *Sarcophilus*. This aim has necessitated a look at many aspects of the morphology, ecology and genetics of *Sarcophilus*, both modern and fossil. These aspects, to be discussed below, include dental morphology, tooth wear, and skull and postcranial skeleton morphology. On this basis the taxonomic status of the several morphologically distinct forms of *Sarcophilus* is considered, and a hypothesis concerning the phylogeny of the genus is presented.

MATERIAL

The material of modern *S. harrisii* used in this paper consists of 30 skulls and mandibles, and 26 skeletons, all from the collections of the Museum of Victoria. Of the 30 skulls, 5 were from animals bred or reared in zoos, and the remaining 25 were caught in the wild in Tasmania between 1859 and 1971, with the majority caught between 1910 and 1917 (only two of these specimens are from the period before the 1908 event to be discussed later). The 26 skeletons, of which 18 were associated with skulls, included only one zoo animal. Summary statistics for this sample are presented in the Appendix, Table 1.

Most of the fossil specimens of *Sarcophilus* used in this paper come from either of two samples. The first, referred to *S. laniarius* by Marshall (1973a), comes from Strathdownie, western Victoria, and includes 28 fragmentary mandibles, 18 maxillary fragments, and one partial humerus. This material was separated into two groups on the basis of which side of the skull each specimen belonged to, and was then examined to determine if any two or more could have belonged to the same individual. In such cases only the more complete side was measured. After the completion of this procedure there remained 23 fragmentary mandibles and 17 maxillary fragments. The summary statistics for this sample are presented in the Appendix, Table 2.

The second major sample of fossil (really sub-fossil) *Sarcophilus* comes from Mt. Hamilton, Victoria. This sample will be referred to in the text as *S. cf. harrisii*. After the procedure outlined above was carried out, there remained 38 mandible fragments and 23 fragmentary maxillae in this sample. It also included 12 skulls complete enough for measurements to be made on them. Summary statistics for this sample are presented in the Appendix, Table 3.

For stratigraphic information on these sites I refer to Merrilees (1965) and Wakefield (1963). The variation within each sample as measured by the coefficient of variation (CV) is in both cases at a level which is reasonable in natural populations (Appendix, Table 2 and 3), and this is sufficient for present purposes, as this analysis lies chiefly at the population, rather than individual, level.

A number of other specimens of fossil *Sarcophilus* from other sites have been examined, but no other single site has produced samples as large as the aforementioned.

MEASUREMENTS

The following is a list of the measurements used in this paper and their respective definitions.

Dentition. LM₂, LM₃, LM₄, LM₅: anteroposterior length of respective molar; WM₂, WM₃, WM₄, WM₅: transverse width of respective molar; HbehM₅: height of mandibular ramus immediately posterior to M₅; LM₂-LM₅: anteroposterior length of lower molar series; JL: length of mandible from front of canine alveolus to back of condyle; LM₂, LM₃, LM₄: anteroposterior length of respective molar; LmM₄: length of metacrista of M₄; WM₂, WM₃, WM₄: transverse width of respective molar at the level of the protocone; LM₂-LM₄: anteroposterior length of molar series excluding M₅.

Skull. C-C: width of snout between external margins of canine alveoli; M⁴-M⁴: width of palate between buccal margins of M⁴; I⁴-I⁴: width of incisor series between outermost incisors; IOF: distance between infraorbital foramina; IOB: least distance between orbital fenestrae; POC: least width across postorbital constriction; NasL: length of nasals; PL: greatest length of palate.

Postcranial skeleton. Hum. W. Shaft: greatest width of the shaft of the humerus at the deltoid ridge; Hum. W. Dist.: greatest transverse width across the distal end of the humerus; Radius W. Dist.: greatest width of the distal end of the radius.

It is most important to realise that, due to differences in the definitions of the variables and in measuring equipment, the dental variables used here are not identical with those used by Dawson (1982), and the two samples can therefore, not be directly compared.

All measurements were taken with dial calipers to the nearest 0.1 mm. In the statistical analyses the raw data were transformed into \log_{10} . The dental terminology follows Archer (1978).

METHODS

Aside from qualitative observations of the morphology of fossil and modern *Sarcophilus*, some quantitative methods were used.

In the analysis of the dental proportions of the major samples, a log ratio diagram was constructed in the manner outlined by Simpson (1941).

For more specific considerations of dental and skeletal variables and their allometric patterns, bivariate regression analyses were carried out. All regression axes are reduced major axes, for which the slope (regression coefficient) is calculated as:

$$K = \frac{S_y}{S_x}$$

where S_x and S_y are the standard deviations of x and y , respectively (Sokal and Rohlf 1981).

The regression axes of two samples were tested for equality of slopes according to the formula:

$$Z_1 = \frac{a_2 - a_1}{\sqrt{(sa_1)^2 + (sa_2)^2}}$$

(Imbrie 1956), where a_1 and a_2 are the slopes of the regression axes of the two samples, and sa_1 and sa_2 are the standard errors of a_1 and a_2 respectively.

The majority of the regression axes tested against each other in the manner detailed above did not differ significantly. They were then tested to determine if they differed significantly in location, using the formula:

$$Z_2 = \frac{x_0(a_1 - a_2) + (b_1 - b_2)}{\sqrt{(sa_1)^2(x_0 - x_1)^2 + (sa_2)^2(x_0 - x_2)^2}}$$

(Imbrie 1956), where a_1 , a_2 , sa_1 and sa_2 are defined as above, b_1 and b_2 are the x^- intercepts of the two samples, x_1 and x_2 are the means of the x^- variables in the two samples, and x_0 is a point on the x^- axis. In the present study the null hypothesis in any comparison was that the samples were not significantly different. To produce the most stringent test of this hypothesis, x_0 was selected as that point within the range of overlap of two samples at which the difference between them was greatest.

Both tests are z^- tests, and significance levels were found by inspection of tables of the normal distribution function.

RATIO ANALYSIS

In a ration analysis comparing modern *S. harrisii* from Tasmania with a sample of *S. laniarius* from Wellington Caves, New South Wales, Dawson (1982) found that the molars of the latter were relatively longer, and that this difference increases posteriorly in the tooth row.

Dawson (1982) used this difference in proportions to justify a specific separation between the modern and the fossil taxon. I have duplicated the ratio analysis of Dawson (1982), with the addition of the sample of *S. cf. harrisii* from Mt. Hamilton, which is ostensibly identical with the modern form. The results of this analysis are presented in Fig. 1. The comparison between *S. harrisii* and *S. laniarius* shows essentially the same differences as those obtained by Dawson (1982), despite the slight difference in the measurements. Thus, the molars of *S. laniarius* are progressively longer towards the rear of the tooth row, with the exception of M_3 . The deviation of M_3 from the general pattern can also be seen in Dawson (1982, Fig 1), although to a lesser degree.

A comparison between modern *S. harrisii* and *S. cf. harrisii* from Mt. Hamilton shows that the same differences in molar proportions separate these two groups as separate *S. harrisii* from *S. laniarius*. The two fossil samples, on the other hand, differ only in size, not in proportions. There are no grounds for separating these two forms at the species level on the basis of dental proportions.

DENTAL REGRESSION ANALYSIS

Bivariate regression analysis was performed on a total of 24 dental variable pairs. When the correlation coefficient between two variables is not significant, the reduced major axis is not defined, and consequently the number of pairwise comparisons in no case reaches the maximum possible. As stated in the methods section, a variable pair was first tested for difference in slopes between two samples. If the samples did not significantly differ, they were then tested for difference in location. Variable pairs for which two samples were significantly different in the regression slopes were not tested again.

The overall results of the significance tests are shown in Table 1. All three samples differ from each other in a large number of comparisons. Of particular note is that modern *S. harrisii* and *S. cf. harrisii* from Mt. Hamilton differ significantly from each other in 11 out of 14 comparisons (79%). The Mt. Hamilton and Strathdownie samples, on the other hand, differ from each other in a lower percentage of comparisons (50%), confirming to some extent the finding of the ratio analysis that these samples differ mainly in size, and less in proportions.

Figs. 2A-F show some examples of the growth patterns encountered in the samples.

Fig. 2A shows the regression LM^4/LM^2-M^4 . *S. cf. harrisii* from Mt. Hamilton differs significantly in slope from both the other samples, which in turn differ significantly from each other in the location of the regression axis. Thus, *S. laniarius* has the longest molar tooth row relative to M^4 length, and *S. cf. harrisii* the shortest, but this difference decreases with size, as large specimens of the latter sample have relatively longer molar tooth rows. Although this is based on a static allometric pattern, I would still suggest that it may be due to a difference in the timing of eruption of M^4 . If this tooth erupted earlier in *S. cf. harrisii* the individuals would be smaller at eruption, and there would be less room for the tooth, leading to a greater imbrication of the posterior molars, an imbrication which would decrease as the mandible grew to full size.

In the next figure, Fig. 2B, is shown the regression of LM_2/WM_2 . Here there are no differences in slopes, but *S. cf. harrisii* differs significantly from the other two samples in having a relatively broader M_2 . *S. harrisii* and *S. laniarius* do not differ significantly from each other.

The regression LM_3/LM_4 (Fig. 2C) shows that there are significant differences in the relationship of the lengths of these two teeth between all three samples. The M_4 of *S. laniarius* is the longest relative to M_3 of the three samples, while M_4 is shortest in *S. harrisii*.

The regression of LM^3/LM^2-M^4 (Fig. 2D) shows essentially the same pattern as in Fig. 2A, but here the differences between the samples are smaller. All three comparisons of locations were significant, however.

Fig. 2E shows the regression LM_4/LM_2-LM_5 . In this regression, *S. cf. harrisii* differs significantly from the two other samples. As the figure shows, M_4 of *S. cf. harrisii* is relatively longer than in either *S. harrisii* or *S. laniarius*.

The final regression figured is LM_3/W_3 (Fig. 2F). *S. harrisii* and *S. lanarius* differ significantly from each other in the slope of the regression axes. In addition, *S. cf. harrisii* differs from both other samples in the location of the axis. the figure shows that *S. lanarius* has the broadest M_3 , while that of *S. harrisii* is the narrowest. Note especially the great difference in M_3 width between *S. harrisii* and the Mt. Hamilton sample.

Dawson (1982) observed that some late Pleistocene specimens of *Sarcophilus* were significantly smaller than modern *S. harrisii*. Specimen MV P171590 (B in Figs. 2A, 2D, see also Fig. 8) from Nelson, Victoria, is an additional such specimen. It differs in size from modern *S. harrisii* to about the same extent as the latter does from *S. lanarius*. In dental proportions it seems more closely allied to *S. cf. harrisii* providing some support for Dawson's (1982, Fig. 3) Hypothesis 1 concerning the late Pleistocene evolution of the genus.

There is one further specimen which may belong to the small form of *Sarcophilus*. This is MV P1857, from Gisborne, Victoria (H in Figs. 2B, 2C, 2E, 2F). This specimen was first described by McCoy (1882).

Another specimen, MV P15285 and 15286 (skull and mandible of a single individual, A in Figs 2A-F), from Lake Corangamite, Victoria, is interesting in that it takes up a position intermediate between *S. lanarius* and *S. harrisii* in some features of the dentition (e.g. Figs 2A, 2D). The specimen seems nearer to the latter species, however, and is here tentatively referred to *S. cf. harrisii*.

All other specimens included in Figs. 2A-F, except MV P26544 (C in Figs. 2A, 2D, 2E), previously identified by Marshall (1973a, 1973b) as *S. lanarius*, can be confidently referred to *S. cf. harrisii*. It is clear particularly from Figs. 2C and 2F, that these fossil specimens lie closer to *S. cf. harrisii* from Mt. Hamilton, than to modern *S. harrisii* from Tasmania, indicating that the use of the Mt. Hamilton sample as a fossil representative of a group equivalent in size to modern *S. harrisii* is justified.

CRANIAL REGRESSION ANALYSIS

Very few specimens of *S. lanarius* are complete enough to allow measurements of the skull and mandible to be taken accurately. One such specimen is MV P26544 from Lake Victoria, New South Wales (Marshall 1973a, 1973b). In Fig. 3 this specimen is compared with samples of modern *S. harrisii* and *S. cf. harrisii* from Mt. Hamilton. There were not enough specimens in the latter sample for regression axes to be calculated. Instead, the means and standard errors for the x^- and y^- variables are presented in Figs. 3A-C. Some additional fossil specimens of *Sarcophilus* are also included, among them MV P171590 from Nelson, Victoria, which has been diagnosed as belonging to the distinct small form of *Sarcophilus* on the basis of dental measurements (see above).

Only a few measurements could be taken on MV P26544. The available evidence indicates that the posterior width of the palate (M^4-M^4) was greater in *S. lanarius* than in the other two samples (Fig. 3A). MV P26544 has, however, been damaged in this region, and has subsequently been repaired. A small error in this restoration will have a large effect on the measurement M^4-M^4 , and the observed pattern can therefore not be taken as indicative of a morphological difference between the two forms.

It can be observed in Figs. 2A, 2D and 2E that MV P26544 is small in dental dimensions for a specimen of *S. lanarius*, smaller in fact, than any specimen from the Strathdownie site. It is larger in upper dental dimensions than any specimen of modern *S. harrisii* in the sample used by me, however, and there is no doubt that it belongs to the larger form, especially as the other specimens from Lake Victoria are clearly within the *S. lanarius* size range (Marshall 1973a). In cranial dimensions, on the other hand, MV P26544 is within the range of modern *S. harrisii*. This suggests either that the specimen is not fully grown, or that *S. lanarius* had relatively large teeth compared with *S. harrisii*, or both. Present evidence is insufficient to allow a more definite statement to be made.

S. cf. harrisii from Mt. Hamilton differs from the modern Tasmanian form in a number of ways. Most important of these is that the left and right tooth rows of the Mt. Hamilton form are more nearly parallel than in the modern form. This is best seen in Fig. 3B, which shows that *S. cf. harrisii* is broader across the canines than the modern form, but that the two are almost identical in the width of the posterior part of the palate.

Another difference between *S. cf. harrisii* and the modern form is in size. That the Mt. Hamilton form is larger is readily seen in Fig. 3A (10F) and 3B (C-C), but is clearest in the diagram of 10F against 10B (Fig. 3C). The means of both these variables are greater in *S. cf. harrisii* than in *S. harrisii* from Tasmania. This is another demonstration of the complex pattern of size differences between different groups of fossil, sub-fossil and modern *Sarcophilus*. Posterior width of the palate is, as noted above, an exception to the pattern of greater size of the fossil form, indicating that the relative narrowness of the palate in *S. cf. harrisii* is the feature responsible for the more parallel tooth rows in this form (Figs. 3A, 3B).

Specimen MV P171590 agrees in all variable pairs with *S. cf. harrisii* (Figs. 3A-C). This is what we would expect if Dawson's (1982) Hypothesis 1 concerning the evolution of *Sarcophilus* is correct. Unfortunately, *S. laniarius* is too poorly known cranially to allow comparisons to be accurately made. The observed pattern also highlights the dangers of using modern *S. harrisii* in comparisons with fossil or sub-fossil forms. If such a comparison had been made, the conclusion that MV P171590 differs significantly from *S. harrisii* in skull shape would have been inescapable. As it is, the observed differences between these two forms are tempered by the presence of an intermediate form, similar to MV P171590 in proportions, but similar to modern *S. harrisii* in size.

A final important feature to note in connection with MV P171590 is that, while the teeth of this specimen are much smaller than those of *S. harrisii* (Figs. 2A, 2D), the skull is only slightly smaller (Figs. 3A-C), suggesting that the fossil form to which this specimen belongs had relatively small teeth.

POSTCRANIAL REGRESSION ANALYSIS

No previous study of *S. laniarius* (or other fossil *Sarcophilus*) has to my knowledge taken the postcranial skeleton into account. The material at my disposal includes postcranial elements of several individuals, including a partial skeleton associated with the skull MV P26544 from Lake Victoria, New South Wales. The postcranial elements of this specimen are listed in Table 2. In addition, two other specimens were available. Both are partial humeri, and both come from sites at which *S. laniarius* has been identified on the basis of dental remains. They are MV P173149 from the Strathdownie site, and MV P29547 from Keilor, Victoria (Marshall 1974). These specimens are illustrated together with the humerus of a modern *S. harrisii* in Fig. 4.

Very few measurements could be taken on any of these postcranial elements. Aside from the humeri and the radius of MV P26544, only measurements of foot bones could be taken, and then only lengths. Since there is a possibility that MV P26544 is not fully grown, these latter measurements have not been analysed here. Only one measurement, width of the shaft, could be taken on all humeri. This measurement indicates (Table 3) that MV P26544 is very small for a specimen of *S. laniarius* and thus confirms the conclusions drawn from the skull measurements.

MV P26544 is naturally of particular interest, as it is the only one of the three to be associated with skull and dental remains. In Figs. 5A and 5B, the distal width of the radius and shaft width of the humerus, respectively, are compared with IOF. Since no postcranial material of *S. cf. harrisii* was available, these figures include only modern *S. harrisii* and *S. laniarius*. MV P26544 lies clearly outside the range of *S. harrisii* in Fig. 5A, while in Fig. 5B it lies near where an average *S. harrisii* of that size would be expected to lie. Together the two diagrams indicate that, while the shaft width of the humerus and IOF follow the allometric pattern of *S. harrisii*, distal width of the radius does not. The latter is much greater in MV P26544 than would be expected in an individual belonging to *S. harrisii*.

MV P173149 from Strathdownie is the only humerus on which two measurements, shaft width and maximum distal width, could be taken. This specimen is compared with *S. harrisii*, and the result is shown in Fig. 5C. The fossil specimen differs from the modern in that the humerus is relatively narrow distally

Regarding *S. harrisii*, it is worth noting that both Fig. 5B and 5C show that the shaft width of the humerus increases more rapidly than either IOF (Fig. 5B) or distal width of the humerus (Fig. 5C). This is expected, as shaft width of the humerus is a rough estimate of the weight bearing capacity of that bone, and should therefore increase as the mass of the animal, rather than its linear dimensions. Fig. 5C shows that the shaft width of the large *S. lanianus* was even greater than in *S. harrisii* of equivalent size.

DENTAL WEAR

The sample of *S. lanianus* from Strathdownie was examined with regard to dental wear. The following discrete stages of molar wear could be identified.

Lower dentition

Stage 1. (Fig. 6A). The paraconid of M₂ is higher than the protoconid. Both these cusps are clearly distinguishable on M₃, although all three are worn. A wear facet is just beginning to develop on the paraconid and protoconid of M₄, and a buccal wear facet is clearly but weakly developed on this tooth. The cusps of M₅ are unworn and the buccal wear facet of this tooth is just starting to develop.

Stage 2. (Fig. 6B). M₂ is worn flat and its occlusal wear facet is inclined posteriorly. The paraconid and protoconid of M₃ are worn down to the same level. There is marked wear on the cusps of M₄, and the buccal wear facet of this tooth almost reaches the tip of the protoconid. Wear is commencing on the cusps of M₅, and its buccal wear facet is now very distinct.

Stage 3. (Fig. 6C). The previously flat wear facet on M₂ is now distinctly concave. M₃ is worn flat and the occlusal wear facet is nearly horizontal. M₄ is worn blunt, with the protoconid worn down to the level of the paraconid of M₅. The buccal wear facet of M₄ includes the tip of the protoconid. The paraconid and protoconid of M₅ are clearly worn and the notch between them is beginning to open up. The buccal wear facet of M₅ almost reaches the tip of the protoconid.

Stage 4. (Fig. 6D)). (Only M₅ is known for this stage of dental wear in *S. lanianus*.) The paraconid and protoconid are becoming blunt, and the notch between them is very wide. The buccal wear facet includes the tip of the protoconid.

Upper dentition

Stage 1. Very slight wear is present on the tip of P². The metacone and tips of the protocone and paracone of M² are worn. The wear on M³ is slight. A lingual wear facet is beginning to develop on this tooth. M⁴ is not worn, and its lingual wear facet has not yet begun to develop.

Stage 2. The tip of P² is well worn. The metacone of M² is worn and approaching the level of the paracone. The metacone and paracone of M³ are worn, and the metacone shear is nearly obliterated. The protocone of M³ is slightly worn. M⁴ is slightly worn, with a distinct lingual wear facet.

Stage 3. P² is worn down to $\frac{2}{3}$ its original height, and is now level with M². The paracone and metacone of M² are worn flat, almost to the level of the protocone. The paracone and metacone of M³ are worn flat to the same level, and metacone shear is obliterated. M⁴ is well worn, with metacone shear nearly obliterated.

All the dentitions allocated to wear stage 1 were mature, with all teeth fully erupted.

It is tempting to identify these discrete wear stages with age classes separated by one year intervals. Indeed, in view of how distinct the stages are, it is difficult to see what else they could

be. This would in turn indicate that deposition at Strathdownie was either seasonal or occurred only once, as otherwise individuals of different ages would be expected to be present in the material, and the stages consequently obliterated. This is the situation in the Mt. Hamilton material, as far as I have been able to determine. However, there is no evidence available from the literature regarding the time of complete eruption of the postior most molars in *Sarcophilus*, the only relevant work on this subject terminating at a much earlier stage of tooth eruption (Guiler and Heddle 1974). In a specimen of *Thylacinus cynocephalus* in the collections of the Museum of Victoria (MV C5600), labeled as being 18 months old at the time of death, M⁴ is still erupting. A similar time for the full reupction of all molars may pertain in the case of *Sarcophilus*. In the wild today, devils live to around 6-7 years of age (Guiler 1978). Until data enabling dating of the Strathdownie specimens becomes available, the hypothesis that the wear stages represent year classes must remain in doubt.

I have not been able to determine if similar wear stages are present in modern *S. harrisi*. The sample at my disposal consisted of specimens collected at different times of the year. When this is the case, discrete wear stages would not be expected, nor were any seen.

TAXONOMIC STATUS OF FOSSIL DEVILS

The previous sections of this paper have presented a range of data on the morphology of modern, sub-fossil and fossil *Sarcophilus*. At this stage it is appropriate to consider the taxonomic status of the several groups of fossil devils that have been identified.

There are at least three distinct fossil and sub-fossil forms of *Sarcophilus* present in the material. The first of these has, for the sake of convenience, been identified as *S. cf. harrisi* in the analyses, and comes from Mt. Hamilton, Victoria, as well as a few other late Pleistocene and Holocene sites. The second form comes from Strathdownie, Lake Victoria and Keilor, and has above been identified as *S. laniarius*. The third form comes from a few localities in southeastern Australia. This form has previously been identified by Dawson (1982).

All these three groups differ significantly from *S. harrisi* as that species appears today. The three major samples on which most of this paper is based differ from each other in a great many variables. It should be noted, however, that the number of significant differences may be somewhat exaggerated in the case of *S. harrisi*, due to the very low variability of this sample (Appendix, Table 1). Nevertheless, all three samples are morphologically distinct, and differ also from the small form (Dawson 1982).

It must now be decided at what, if any, taxonomic level the three forms should be separated from each other and from the modern form. The three are approximately equidistant from each other in size, and differ only slightly in dental and skeletal proportions (cf. Fig. 1-3, 5). These differences in proportion are so minor as to be clearly inadequate for separation at the species level. Previous separation between *S. harrisi* and *S. laniarius* has been based chiefly on the difference in size, with cited differences in proportions and morphological features being discounted by subsequent authors (Owen 1877, Marshall 1973a, Dawson 1982, this paper). Until such a time as positive evidence for sympatry without evident interbreeding between large and small devils has been uncovered, I consider size in itself to be an inadequate taxonomic indicator at the species level. The size difference between *S. harrisi* and *S. laniarius* is approximately the same as between modern South American *Felis wiedii* and fossil North American *F. amnicola*, which I have elsewhere considered conspecific (Werdelin 1985), and is considerably less than between the Eurasian lynx, *Lynx lynx* and the Spanish lynx, *L. pardina*, which by several authorities (Ellerman and Morrison-Scott 1951, Corbet and Hill 1980) are considered conspecific (albeit perhaps incorrectly, cf. Delies 1980, Werdelin 1981). The idea that these fossil and sub-fossil *Sarcophilus* represent separate species must therefore be rejected at the present time. At the same time, it is undeniable that there are differences between them, differences suggesting restricted gene flow (geographical or temporal), and subspecific rank seems appropriate to express these differences.

When there were only two taxa, large *S. laniarius* and small *S. harrisi*, separation at the species level could be justified, as both size differences and differences in proportions were

involved. We now also have *S. cf. harrisii*, however, which is almost equal in size to the modern form, but different in proportions (cf. Figs. 2, 3). Fig. 1 shows that these differences in proportions are precisely those which also separate modern *S. harrisii* from fossil *S. laniarius*. In my opinion, *S. cf. harrisii* must be accorded subspecific status separate from modern *S. harrisii*. This opinion is based on the following reasoning: (1) *S. harrisii* and *S. cf. harrisii* differ significantly from each other in a number of dental and skeletal features. (2) Most of these differences also distinguish *S. laniarius* from *S. harrisii*. (3) Size is the single most important distinguishing feature between *S. cf. harrisii* and *S. laniarius*. (4) We cannot give the size difference between *S. laniarius* and *S. cf. harrisii* more weight than the differences in proportions between *S. harrisii* and the other two samples. (5) Thus, if we consider *S. harrisii* and *S. cf. harrisii* subspecifically identical, then the latter form and *S. laniarius* must also be subspecifically identical. (6) This would make all three subspecifically identical, which is surely not acceptable. (7) I thus conclude that, due to the *S. cf. harrisii* being intermediate in morphology between *S. harrisii* and *S. laniarius*, all three must be acknowledged as taxonomically distinct.

The failure to recognize the distinctness of *S. cf. harrisii* is precisely that which has led Dawson (1982) to consider *S. harrisii* and *S. laniarius* as separate species. This is incorrect, as I have tried to show above, and subspecific status for *S. cf. harrisii* may help avoid this error in the future.

NOMENCLATURE

The Tasmanian devil was first described by Harris (1808) under the name of *Didelphis ursina*. However, as pointed out by Thomas (1903), this name is preoccupied by *Didelphis ursina* Shaw 1800, the common wombat, and thus not available for devils. Thomas (1903) substituted the name *Sarcophilus satanicus* for *S. ursinus*, but later (Thomas 1912) pointed out that the earlier name *Ursinus* (= *Sarcophilus*) *harrisii* Boitard 1841, overlooked in his 1903 publication, was available. This name has since been used for the living Tasmanian devil. For the large fossil form the name *Sarcophilus laniarius* Owen 1838 has been used.

If the evidence presented here that the large fossil *Sarcophilus* from Strathdownie (Marshall 1973a, this paper), Wellington Caves (Owen 1838, Dawson 1982), Lake Victoria (Marshall 1973a, 1973b) and other Pleistocene sites is conspecific with the modern Tasmanian form is accepted, then the earlier name *S. laniarius* becomes the valid name for the living form as well, and *S. harrisii* becomes a junior synonym (not senior, *pace* Archer et al. 1984).

The diagnoses have presented something of a problem, as the differences between the subspecies are based mostly on statistical parameters. The diagnoses below present characters which, when analysed statistically with the aid of samples of most forms, should allow most, if not all, individual specimens, even if found without a stratigraphic context, to be allocated to the correct subspecies. allocation of mammal specimens to subspecies merely on the basis of visual inspection of skull and dental features is rarely if ever possible, and is not so in the present case.

Family: Dayuridae Goldfuss, 1820
Genus: *Sarcophilus* Geoffroy and Cuvier, 1837
Species: *S. laniarius* Owen, 1838
Subspecies: *S. l. laniarius* Owen, 1838.

Diagnosis: Subspecies 16% larger than the modern *S. l. harrisii* (average over 17 dental measurements). Average WM_3/LM_3 index 62.3 ± 0.4 (mean \pm standard error) (cf. Fig. 2F). Average LM_3/LM_4 index 82.5 ± 0.7 (cf. Fig. 2C). Average LM_4/LM^2-LM^4 index 36.1 ± 0.4 (cf. Fig. 2A).

Comments: This subspecies has been known for a long time and can be readily identified on the basis of dental and cranial material. The postcranial skeleton is as

yet poorly known. The known remains come from Victoria, New South Wales, South Australia and Western Australia (J. Hope, pers. comm.).

Subspecies: S. l. harrisii Boitard, 1841

Diagnosis: Average WM_3/LM_3 index 57.8 ± 0.3 (cf. Fig. 2F). Average LM_3/LM_4 index 90.5 ± 0.3 (cf. Fig. 2C). Average LM_4/LM^2-LM^4 index 35.6 ± 0.1 (cf. 2A).

Comments: This subspecies is the living Tasmanian devil. It has no known fossil representatives. Study of fossil and sub-fossil remains of *Sarcophilus* found on Tasmania may help resolve whether it has evolved *in situ* in Tasmania, or whether representatives of this subspecies once lived on the mainland and subsequently became extinct there.

Subspecies: S. l. dixonae ssp. nov.

Diagnosis: Subspecies of a size approximately equivalent to the modern *S. l. harrisii*. Average WM_3/LM_3 index 61.5 ± 0.5 (cf. Fig. 2F). Average LM_3/LM_4 index 87.4 ± 0.6 (cf. Fig. 2C). Average LM_4/LM^2-M^4 index 37.9 ± 0.2 (cf. Fig. 2A).

Holotype: Museum of Victoria P157484, an incomplete skull from Mt. Hamilton, Victoria (Fig. 7).

Type locality: Mt. Hamilton, Victoria.

Etymology: After Joan M. Dixon, Museum of Victoria.

Comments: This subspecies has previously been considered taxonomically identical with the living form. Its geographic range cannot be determined at present, as each known sample must be analysed separately and compared with other samples.

The small form remains to be discussed. I shall refrain from naming this form, as the material I have had at my disposal is very small (only two specimens), whereas other material, both described (Dawson 1982) and undescribed (J. Hope pers. comm.) is considerably more complete. Devils smaller than the modern form have been reported from New South Wales and South Australia (Dawson 1982), Victoria (this paper), Queensland (Horton 1977), Northern Territory (Calaby and White 1967) and Western Australia (J. Hope pers. comm.). Whether all these belong to the same taxon must remain unclear. This material is being studied by J. Hope and K. Aplin (work in progress). In the meantime, Fig. 8 is a photograph of MV P171590, from Nelson, Victoria, here identified as belonging to the small form discussed by Dawson (1982).

RECENT *S. HARRISII* IN THE EVOLUTIUON OF *SARCOPHILUS*

Before presenting a hypothesis of phylogeny of *S. laniarius*, I wish to briefly consider the status of the living Tasmanian *S. l. harrisii* in relation to these topics. Most previous work on the evolution of the genus *Sarcophilus* has been either based on the assumption that its late Pleistocene phase can be characterized by phyletic size decrease (Marshall 1973a, 1973b; Marshall and Corruccini 1978), or has at least arrived at that conclusion on the basis of differences between *S. l. laniarius* (i.e. the large fossil form) and modern *S. l. harrisii* from Tasmania. A dissenting opinion can be found in Dawson (1982), where it is suggested that the modern form instead evolved from a previously unrecognized smaller fossil form. In these analyses it has been tacitly assumed that modern *S. l. harrisii* is taxonomically identical with similarly sized fossil or sub-fossil specimens. While there is no reason to doubt that size is important in the phylogeny of *Sarcophilus* and that similarly sized individuals and populations are closely related, the assumption of identity has eliminated a step in the evolution of *Sarcophilus*, and is especially unwarranted as it is shown herein that the modern form differs significantly in a number of dental and skull characteristics from a sub-fossil sample from Mt. Hamilton, Victoria. I wish here to present a suggestion concerning the history of the modern form of *S. laniarius* during the past 150 years, a suggestion, which if true, is of some import to studies of the evolution of *Sarcophilus*.

Since Europeans first settled in Tasmania, the number of Tasmanian devils on the island has been subject to at least one major decline (Green 1967, Guiler 1985). Around the year 1908 a distemper-like disease swept through the populations, not only of devils, but also of native cats and thylacines, reducing all drastically (Guiler 1985). Over the past 75 years the devil population has slowly recuperated, and the species is now once again common in Tasmania.

The recovery time has been long (some 50 years or more to reach pre-disease population levels), suggesting that the immediate post-disease populations were very small, especially if effective population size is considered. Such population bottlenecks can result, through founder effects and genetic drift, in a reduction of genetic variability and random phenotype changes (Lewontin 1974, O'Brien *et al.* 1983, Boitani 1984). At the phenotypic level there are three main effects (Franklin 1980): (1) a decrease in genetic variance; (2) random phenotype changes, especially in the means of quantitative traits, suggesting faster evolutionary rates; (3) inbreeding depression.

A first indication that the bottleneck has in some way affected Tasmanian *S. l. harrisii* lies in the low coefficients of variation observed in this sample (Appendix, Table 1). This material, except for two specimens, is made up of post-disease devils. Variability in *S. l. laniarius* from Strathdownie and *S. l. dixonae* from Mt. Hamilton is, on the other hand, higher (Appendix, Table 2 and 3), suggesting that the reduction in variability may have occurred recently. Much the same pattern was observed by Marshall and Hope (1973) in their study of *Dasyurus maculatus*. A sample of this species from Tasmania showed much less variability than a comparable sample from Victoria.

It is, however, the second of the above mentioned effects which is of greatest importance to the present context. Since we know that devils have been subjected to at least one population bottleneck in recent times, and that such a bottleneck may have random effects on the phenotype, it is clear that modern *S. l. harrisii* is of equivocal status with regard to the Pleistocene and post-Pleistocene evolution of the genus, and cannot be used to determine character polarity in cladistic analyses of the genus. A similar situation with regard to Indian lions has been described by Todd (1965).

It should be noted, however, that population bottlenecks are generally associated with an increase in phenotypic variability (Wayne *et al.* 1986), due to inbreeding. This is an argument against the idea presented here, but I nevertheless feel that some connection between the known bottleneck and the observed low variability is likely.

At the level of the genotype, theoretical effects of population bottlenecks have been studied by Nei *et al.* (1975), who found that the decrease in variability and recovery time are dependent on the size of the bottleneck and the intrinsic rate of population growth, r , of the animal in question. The size of the bottleneck cannot at present be determined in the case of *S. l. harrisii*, but r is low in most larger mammals, suggesting that genotypic effects of a population bottleneck in *S. l. harrisii* should be slow to disappear. Decreased genotypic variability has been demonstrated in a number of species of carnivorous animals, including the cheetah (O'Brien *et al.* 1983, 1985) and the elephant seal (Bonnell and Selander 1974). To my knowledge there have been no comparable studies carried out on the larger dasyurids. A study of fluctuating asymmetry (Van Valen 1962; Wayne *et al.* 1986) might be of value in this context. Unfortunately, such a study was not possible within the scope of the present work.

PHYLOGENY OF SARCOPHILUS

In conclusion, some comments on the phylogeny of the genus *Sarcophilus* are appropriate. These aspects and others concerning the evolution of *Sarcophilus* will be discussed in another context (Hope and Aplin, work in progress). Until this work is completed, there is little to add here to what has been said by previous authors (Stirton 1957, Ride 1964, Crabb 1982) concerning the early history of the genus. Aplin and Hope (work in progress; J. Hope pers. comm.) consider *Glaucodon ballaratensis* and *Sarcophilus moornaensis* to be conspecific and not on the direct evolutionary pathway towards *Sarcophilus*. However,

I shall retain these taxa plus *Dasyurus* as the sister group of *Sarcophilus*. Our current knowledge of the phylogeny of *Sarcophilus* can best be summarized in a cladogram incorporating the various relevant taxa. The only character for which polarity can be determined with some degree of certainty is size, where it is evident by outgroup comparison that it is most parsimonious to consider small size the plesiomorphic state. This character thus forms the basis for the summary cladogram (Fig. 9). As more material becomes available, it should be possible to determine the polarity of other characters, and to corroborate or refute this cladogram.

It should be noted that this cladogram is compatible, both with a scenario including post-Pleistocene dwarfing in *Sarcophilus*, and one which derives the modern form directly from the small one.

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Table 1

| | <i>har</i> | <i>ham</i> | <i>lan</i> |
|------------|-------------|-------------|-------------|
| <i>har</i> | 5/18 | 11/14 | 9/15 |
| <i>ham</i> | 79 | 1/17 | 7/14 |
| <i>lan</i> | 60 | 50 | 1/16 |

Table 1: Pairwise comparisons of regression axes of modern *S. harrisii* (*har*), Mt. Hamilton *S. cf. harrisii* (*ham*), and Strathdownie *S. lanarius* (*lan*). The table is organised so that above the diagonal is shown [no. significant comparisons/total no. of comparisons], and below the diagonal the percentage significant comparisons. The diagonal shows in boldface the number of growth patterns in each form that deviate significantly from isometry.

Table 2

Shafts of left and right humerus
Distal portions of left and right radius and ulna
Short section of shaft of right tibia
Rib fragments
Fragments of caudal vertebrae
Left fore and right hind foot
Fragments of right fore and left hind foot
Vertebral fragments
Skull
Mandible

Table 2: Elements of the skeleton of *S. lanarius* present in specimen no. MV P26544.

Table 3

| Specimen | P26544 | P173149 | P29547 |
|-----------------|--------|---------|--------|
| Variable | | | |
| Hum. W. Shaft | 14.4 | 17.8 | 16.0 |
| Hum. W. Dist | | 28.0 | |
| Radius W. Dist. | a14.7 | | |

Table 3: Measurements of postcranial elements of some specimens of *S. lanarius*.
a = approximate measurement.

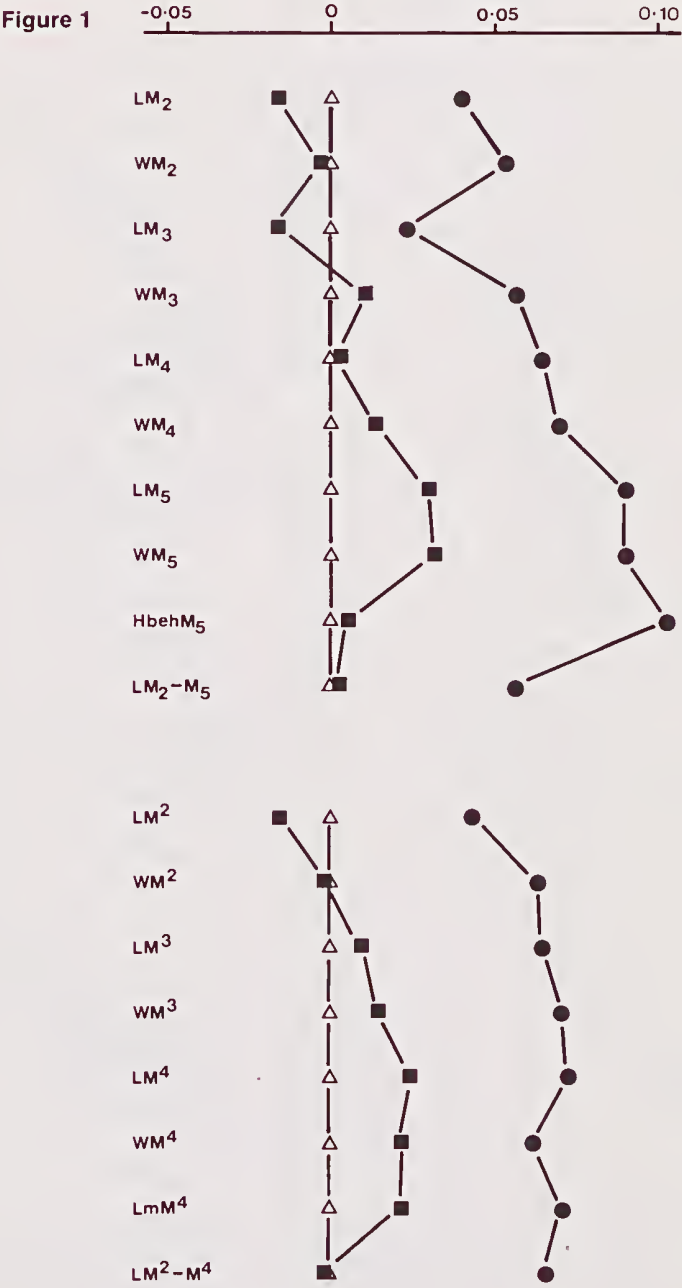


Fig. 1:Ratio diagram of selected samples of *Sarcophilus* (see text). Δ (standard) = modern *S. harrisii*; \blacksquare = *S. cf. harrisii*, Mt. Hamilton; \bullet = *S. lanarius*, Strathdownie. Variable abbreviations are given in the section on measurements.

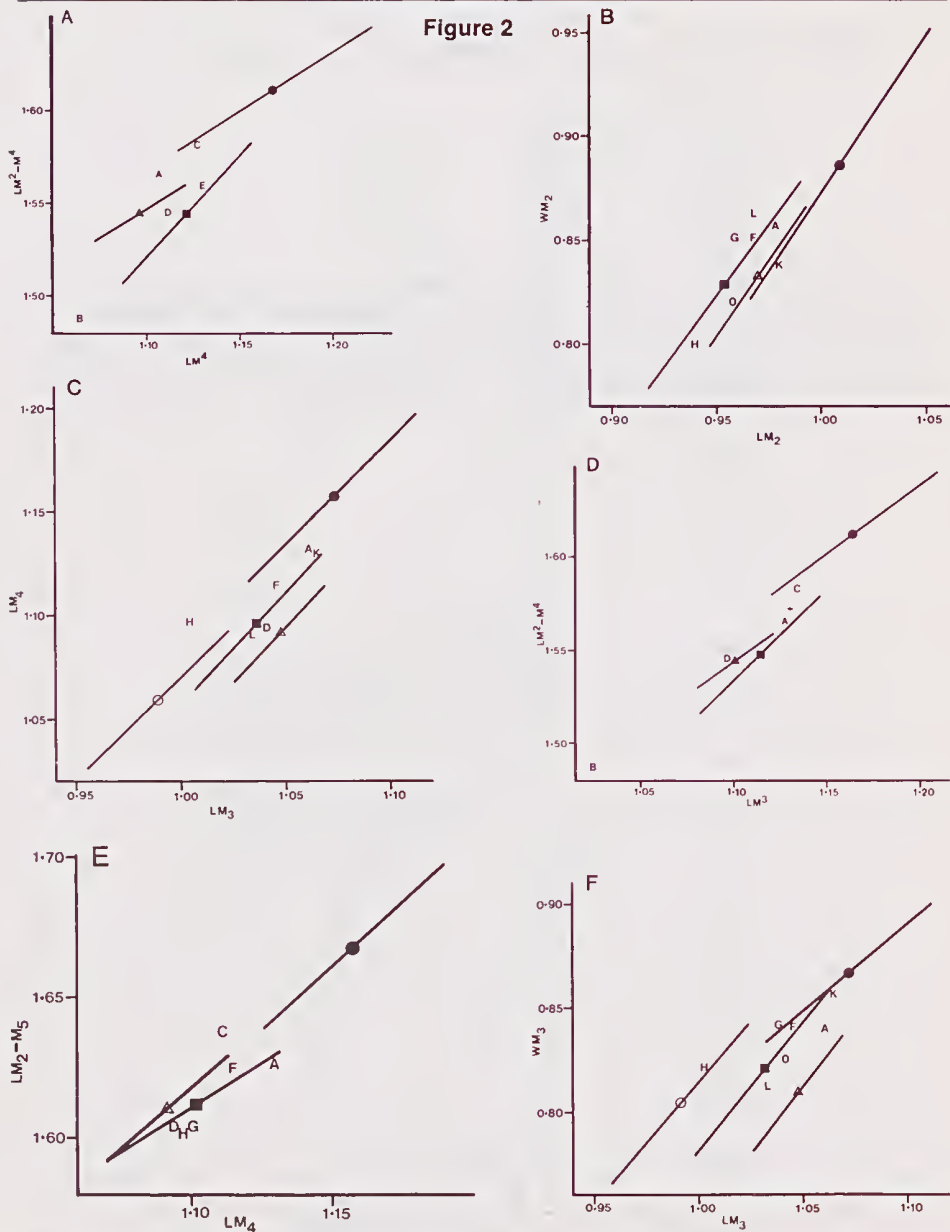


Fig 2: Regression analyses of selected dental variables as discussed in the text. Symbols denote sample means Δ = modern *S. harrisi*; \blacksquare = *S. cf. harrisi*, Mt. Hamilton; \bullet = *S. lanianus*, Strathdownie. A = P15285-6, Lake Corangamite, Victoria; B = P171590, Nelson, Victoria; C = P26544, Lake Victoria, New South Wales; D = P7432, Queenscliff, Victoria; E = P7440, Baringhup, Victoria; F = P30784, Bacchus Marsh, Victoria; G = P26541, Collivers Cave, Victoria; H = P1857, Gisborne, Victoria; K = P24171, Murrindal, Victoria; L = P21421, Tower Hill Beach, Victoria. Variable abbreviations are given in the section on measurements.

Figure 3

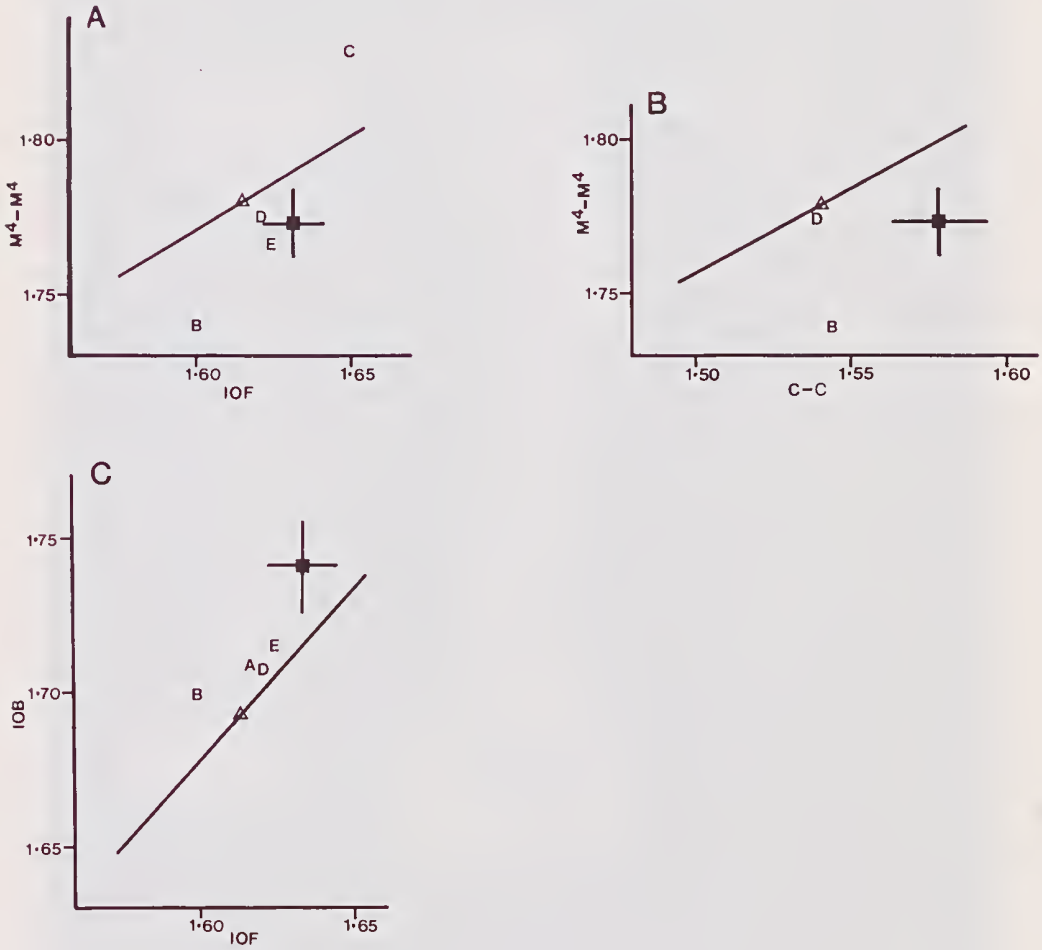


Fig. 3: Regression analyses of selected skull variables as discussed in the text. Δ = modern *S. harrisii*; \blacksquare = *S. cf. harrisii*, Mt. Hamilton. Symbols denote sample means. Alphabetical symbols as in Fig. 2. Variable abbreviations are given in the section on measurements.

Figure 4



Fig. 4: Humeri of (from left to right) P29547 (*S. lanarius*, Keilor), P173149 (*S. lanarius*, Strathdownie) and (reversed) C10907 (modern *S. harrisii*, Tasmania) (x 0.75).

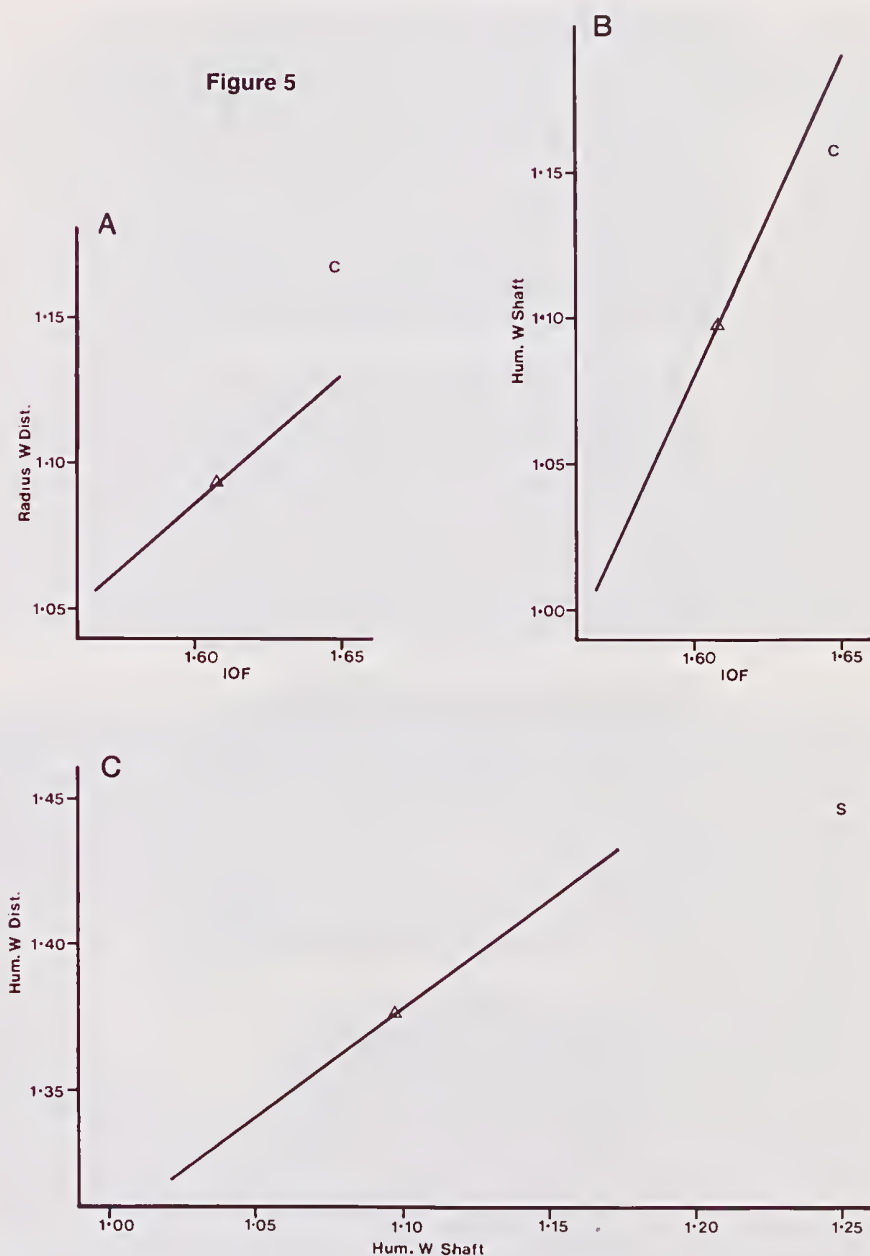


Fig. 5: Regression analyses of selected postcranial measurements as discussed in the text. Δ = modern *S. harrisii*. The symbol denotes the sample mean. C = P26544, Lake Victoria, New South Wales; S = P173149, Strathdownie, Victoria. Variable abbreviations are given in the section on measurements.

Figure 6

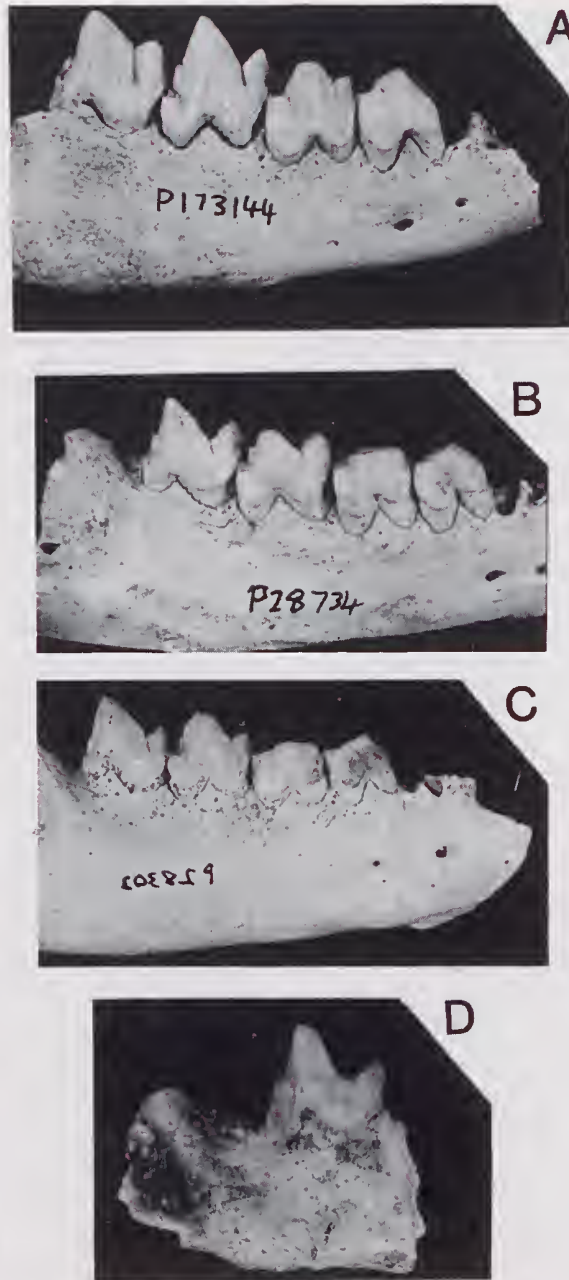


Fig 6: Specimens illustrating (from top to bottom) wear stages 1-4 in the lower dentition of *S. laniarius* from Strathdownie, Victoria (x 1). Stage 3 is reversed from left side.

Figure 7

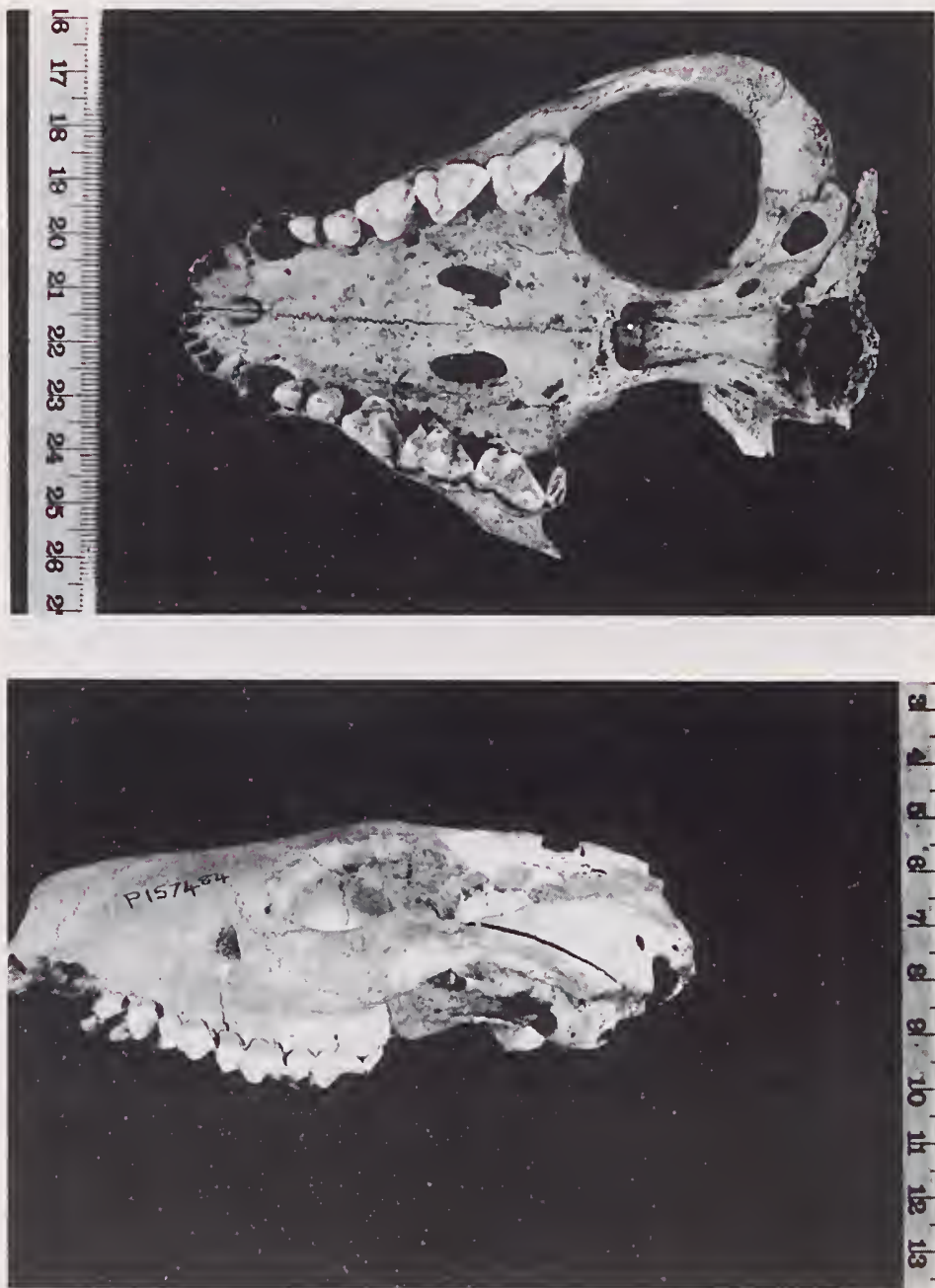


Fig. 7: Ventral and lateral views of P157484, holotype of *S. l. dixonae* ssp. nov. (x 0.50).

Figure 8

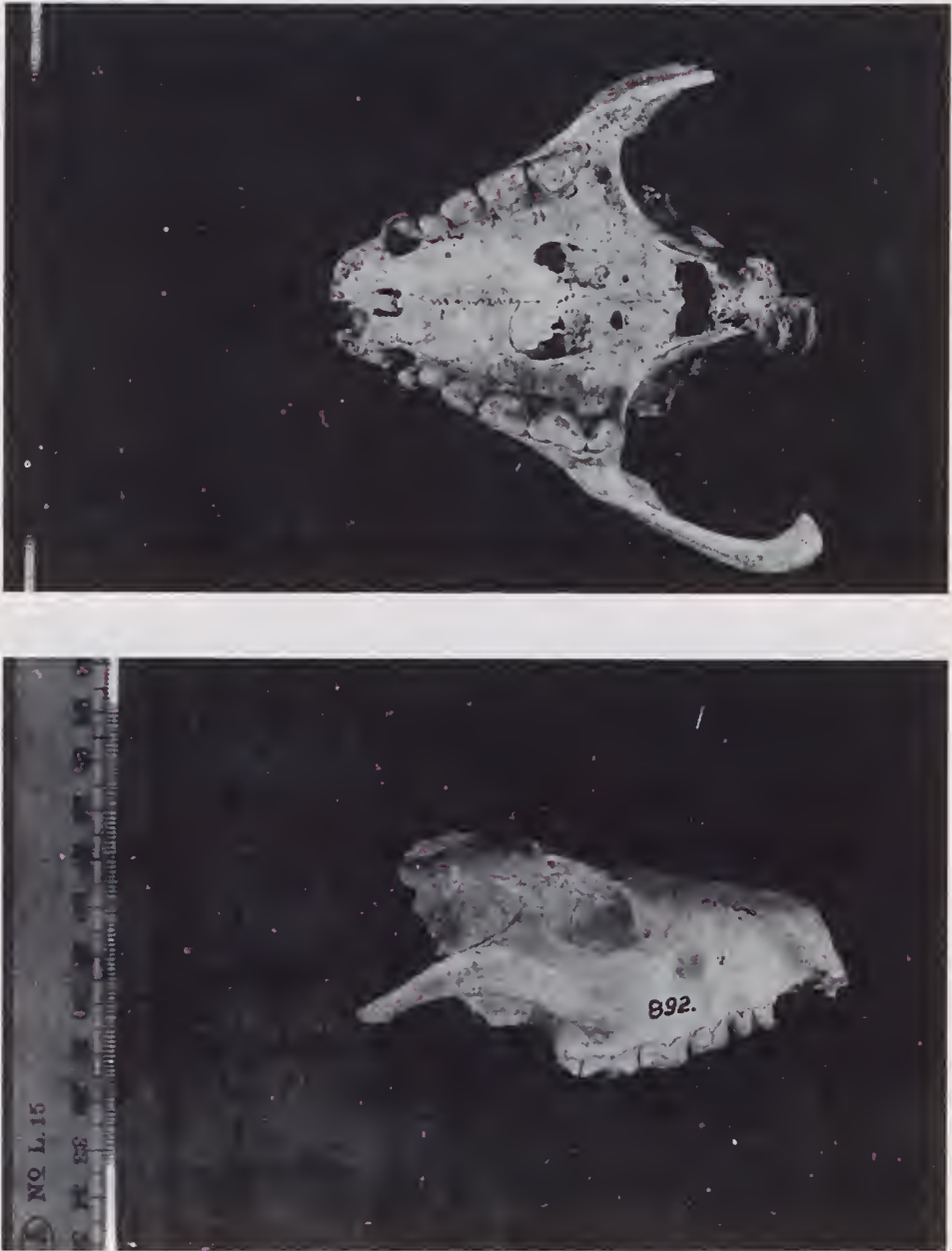


Fig. 8: Ventral and lateral views of P171590 from Nelson, Victoria. (x 0.5).

Figure 9



Fig. 9: Summary cladogram of *Sarcophilus*. Explanation of nodes: 1: Characters of *Glaucodon* + *Dasyurus*. 2: Characters of *Sarcophilus*. (Nodes 1 and 2 are under review, Aplin and Hope, work in progress; J. Hope, pers. comm.). 3: Size increased, teeth relatively larger and longer. 4: Teeth long (especially M_3), muzzle narrow. 5: Size increased still further, teeth relatively larger, humerus more robust.

Appendix, Table 1:
Summary statistics for Recent *S. harrisii*

| Variable | N | \bar{x} | SD | CV | O.R. |
|---------------------------------|----|-----------|-------|------|------------|
| LM ₂ | 30 | 9.33 | 0.245 | 2.63 | 8.8- 9.8 |
| WM ₂ | 30 | 6.80 | 0.264 | 3.88 | 6.4- 7.4 |
| LM ₃ | 29 | 11.18 | 0.277 | 2.47 | 10.6- 11.7 |
| WM ₃ | 29 | 6.46 | 0.206 | 3.19 | 6.0- 7.0 |
| LM ₄ | 30 | 12.36 | 0.325 | 2.63 | 11.8- 13.1 |
| WM ₄ | 30 | 6.44 | 0.271 | 4.21 | 5.9- 7.2 |
| LM ₅ | 27 | 11.59 | 0.483 | 4.17 | 10.7- 12.4 |
| WM ₅ | 28 | 6.06 | 0.282 | 4.65 | 5.7- 6.6 |
| HbehM ₅ | 30 | 22.41 | 1.249 | 5.58 | 20.0- 25.3 |
| LM ₂ -M ₅ | 25 | 40.72 | 0.867 | 2.13 | 39.4- 42.4 |
| JL | 30 | 104.53 | 5.685 | 5.44 | 92.7-117.0 |
| LM ² | 29 | 11.79 | 0.343 | 2.91 | 11.2- 12.4 |
| WM ² | 29 | 9.26 | 0.272 | 2.93 | 8.7- 9.7 |
| LM ³ | 30 | 12.61 | 0.300 | 2.38 | 11.9- 13.3 |
| WM ³ | 28 | 10.03 | 0.343 | 3.42 | 9.0- 10.5 |
| LM ⁴ | 30 | 12.52 | 0.351 | 2.80 | 11.8- 13.2 |
| WM ⁴ | 27 | 10.01 | 0.387 | 3.86 | 9.3- 10.7 |
| LmM ⁴ | 30 | 9.84 | 0.349 | 3.55 | 9.1- 10.4 |
| LM ² -M ⁴ | 29 | 35.09 | 0.613 | 1.75 | 34.0- 36.2 |
| C-C | 24 | 34.76 | 1.901 | 5.47 | 30.7- 40.0 |
| M ⁴ -M ⁴ | 28 | 60.26 | 1.678 | 2.78 | 56.8- 63.7 |
| I4I4 | 27 | 22.10 | 0.972 | 4.40 | 20.8- 24.3 |
| IOF | 28 | 41.12 | 1.925 | 4.68 | 36.9- 45.1 |
| IOB | 28 | 49.38 | 2.589 | 5.24 | 43.3- 54.0 |
| POC | 28 | 18.66 | 1.648 | 8.83 | 15.8- 21.0 |
| NasL | 27 | 50.26 | 3.059 | 6.09 | 45.2- 58.5 |
| PL | 28 | 72.62 | 3.886 | 5.35 | 65.2- 80.9 |
| Hum. W. Shaft | 25 | 12.57 | 1.127 | 8.96 | 10.4- 15.1 |
| Hum. W. Dist. | 25 | 23.81 | 1.609 | 6.76 | 20.9- 28.0 |
| Rad. W. Dist. | 22 | 12.30 | 0.659 | 5.36 | 11.1- 13.5 |

Appendix, Table 2:Summary statistics for *S. lanarius*, Strathdownie

| Variable | N | \bar{x} | SD | CV | O.R. |
|---------------------------------|----|-----------|-------|------|------------|
| LM ₂ | 16 | 10.23 | 0.521 | 5.09 | 9.4- 11.2 |
| WM ₂ | 16 | 7.72 | 0.564 | 7.30 | 6.2- 8.5 |
| LM ₃ | 18 | 11.82 | 0.535 | 4.53 | 11.0- 12.9 |
| WM ₃ | 18 | 7.36 | 0.281 | 3.82 | 6.8- 7.8 |
| LM ₄ | 14 | 14.36 | 0.697 | 4.85 | 13.2- 15.9 |
| WM ₄ | 14 | 7.56 | 0.337 | 4.45 | 7.1- 8.2 |
| LM ₅ | 15 | 14.29 | 0.527 | 3.69 | 13.5- 15.1 |
| WM ₅ | 15 | 7.46 | 0.331 | 4.44 | 7.0- 8.1 |
| HbehM ₅ | 14 | 28.48 | 2.248 | 7.89 | 22.3- 31.1 |
| LM ₂ -M ₅ | 9 | 46.49 | 1.444 | 3.11 | 44.2- 48.0 |
| LM ² | 11 | 13.05 | 0.599 | 4.59 | 12.1- 14.1 |
| WM ² | 11 | 10.72 | 0.389 | 3.63 | 10.4- 11.7 |
| LM ³ | 12 | 14.66 | 0.708 | 4.83 | 13.0- 15.7 |
| WM ³ | 12 | 11.81 | 0.686 | 5.81 | 10.6- 13.1 |
| LM ⁴ | 13 | 14.82 | 0.825 | 5.57 | 13.2- 15.8 |
| WM ⁴ | 13 | 11.56 | 0.578 | 5.00 | 10.2- 12.4 |
| LmM ⁴ | 12 | 11.59 | 0.635 | 5.47 | 10.5- 12.6 |
| Lm ² -M ⁴ | 11 | 40.86 | 1.562 | 3.82 | 37.7- 42.7 |

Appendix, Table 3:

Summary statistics for *S. cf. harrisii*, Mt. Hamilton

| Variable | N | \bar{x} | SD | CV | O.R. |
|---------------------------------|----|-----------|-------|-------|------------|
| LM ₂ | 32 | 9.00 | 0.376 | 4.18 | 8.4- 10.0 |
| WM ₂ | 30 | 6.75 | 0.393 | 5.82 | 5.7- 7.7 |
| LM ₃ | 29 | 10.82 | 0.389 | 3.60 | 10.1- 11.6 |
| WM ₃ | 27 | 6.62 | 0.325 | 4.91 | 6.2- 7.4 |
| LM ₄ | 21 | 12.38 | 0.563 | 4.54 | 11.1- 13.3 |
| WM ₄ | 19 | 6.65 | 0.331 | 4.97 | 6.1- 7.2 |
| LM ₅ | 8 | 12.43 | 0.528 | 4.25 | 11.6- 13.2 |
| WM ₅ | 11 | 6.38 | 0.299 | 4.69 | 5.8- 6.9 |
| HbehM ₅ | 10 | 22.82 | 2.468 | 10.82 | 18.9- 27.9 |
| LM ₂ -M ₅ | 9 | 40.92 | 0.913 | 2.23 | 39.1- 42.3 |
| LM ² | 17 | 11.38 | 0.575 | 5.05 | 10.4- 12.6 |
| WM ² | 23 | 9.32 | 0.540 | 5.79 | 8.2- 10.3 |
| LM ³ | 16 | 12.88 | 0.564 | 4.38 | 12.1- 13.9 |
| WM ³ | 18 | 10.31 | 0.510 | 4.95 | 9.4- 11.2 |
| LM ⁴ | 11 | 13.26 | 0.520 | 3.92 | 12.2- 14.0 |
| WM ⁴ | 12 | 10.52 | 0.420 | 3.99 | 9.7- 11.2 |
| LmM ⁴ | 10 | 10.36 | 0.486 | 4.69 | 9.7- 11.1 |
| LM ² -M ⁴ | 11 | 35.03 | 1.526 | 4.36 | 32.3- 37.3 |
| C-C | 11 | 38.12 | 4.138 | 10.85 | 30.3- 41.8 |
| M ⁴ -M ⁴ | 6 | 59.37 | 3.562 | 6.00 | 55.7- 63.9 |
| I4-I4 | 6 | 24.07 | 1.102 | 4.58 | 23.0- 26.0 |
| IOF | 10 | 43.21 | 3.254 | 7.53 | 36.4- 46.8 |
| IOB | 6 | 55.30 | 4.631 | 8.37 | 47.8- 60.7 |
| POC | 2 | 18.95 | | | 17.7- 20.2 |
| NasL | 3 | 52.33 | 1.976 | 3.78 | 50.2- 54.1 |
| PL | 3 | 82.83 | 3.017 | 3.64 | 80.8- 86.3 |

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